STRENGTH AND DESIGN OF SHELLS OF THE TWO ECOLOGICALLY DISTINCT BARNACLES, *BALANUS BALANUS* AND *SEMIBALANUS* (*BALANUS*) *BALANOIDES* (CIRRIPEDIA)

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The principal function of the shell of the barnacle is to protect the animal from mechanical damage and predation. It has other functions. Some are physiological: to provide thermal insulation, and to prevent water flux inward from hypotonic estuarine or rain water, or outward when the animals are exposed to air. Some are anatomical: to support the animal's body and provide sites of muscle attachment so that the animal can feed and perform other activities effectively. These latter activities could be carried out with fairly delicate structures, however, so the rather thick exoskeletons of barnacles are presumably designed mainly to resist mechanical damage.

Different species of barnacles in the same part of the world may have characteristically different shells, so it is relevant to enquire whether these different shells have different mechanical properties. This paper shows that the shells of the two barnacles, *Balanus balanus* (L.) and *Semibalanus balanoides* (L.) (= *Balanus balanoides*) have remarkably different strengths. This difference is most probably due to differences in general architecture of the shells rather than to microstructure and mechanical properties of the shell material. The architectural and mechanical differences between these two species are best understood in the context of their ecology and life histories.

Barnes, Read, and Topinka (1970) reported on the strengths of the shells of nine species of barnacles. They concluded that shell strength was a function of species, of shell size and of the geometry of the junctions between adjacent wall plates. They found an apparent relationship between shell strength and their ideas of the mechanical demands from waves and wave-washed debris in the habitats typical of the species they discussed.

MATERIALS AND METHODS

Mechanical testing

Specimens of *Semibalanus balanoides* from the mid to low intertidal and *Balanus balanus* from the subtidal were collected from the waters of the Clyde Estuary, Scotland, and kept in tanks of chilled sea water at the University of York. The barnacles were kept on their various natural substrata: the shells of the winkle, *Littorina littorea*; the scallop, *Chlamys* sp.; the mussel, *Mytilus edulis*; the clam *Venerupis pullastra*; and on rock. The tests were made with an Instron table model testing machine. The shell or rock to which the specimen was attached was rigidly fixed so that the opercular opening was horizontal. The shell was loaded
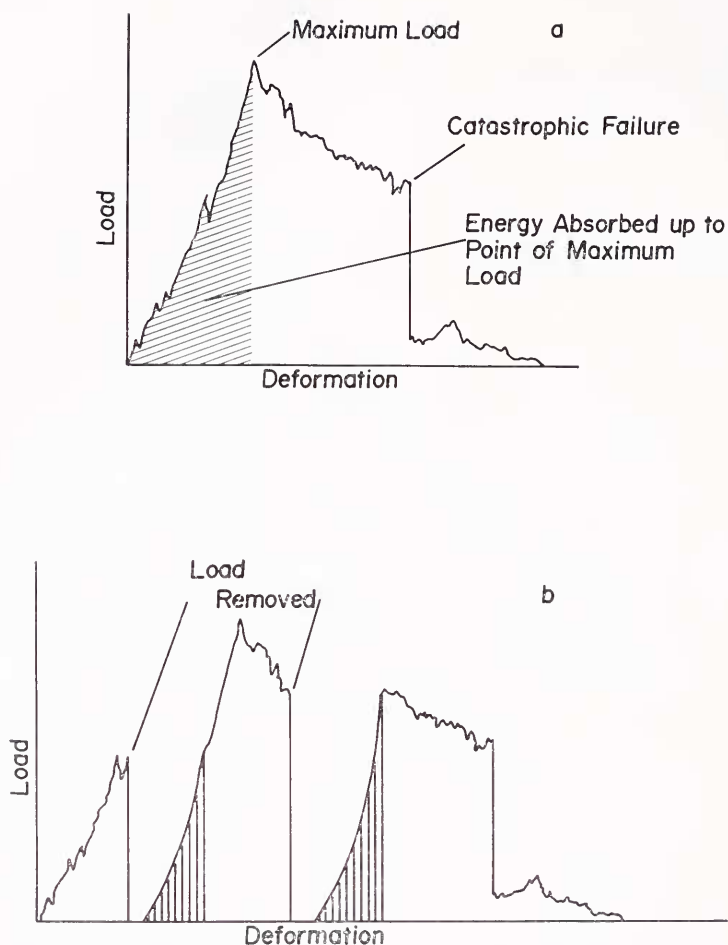
FIGURE 1. Idealized load-deformation curve for a barnacle shell strength test on the Instron. Part a shows a test trace run without pausing or as reconstructed from a test with pauses. The diagonal shading indicates the work done on the specimen up to the point of maximum loading which is the same as the energy absorbed by the specimen. Part b shows the trace obtained when there were pauses in the test (the first two vertical drops in the trace) during which the load was removed. On resumption of the test, the area under the curve up to the last value recorded before the pause (vertical shading) was ignored.

on the rim of the opercular opening by the flat end of a stainless steel cylinder on the moving head of the Instron. The shells chosen for loading were regular in shape and were hardly, if at all, buttressed by the shells of neighbors. When the base of a shell did touch another animal's shell, it was tested only if we considered that the amount of support given was trivial. Those *S. balanoides* occurring on *Littorina* had a regular shape, being small compared with the shell on which they sat.

Before the test was started, the length and breadth of the shell at the base were
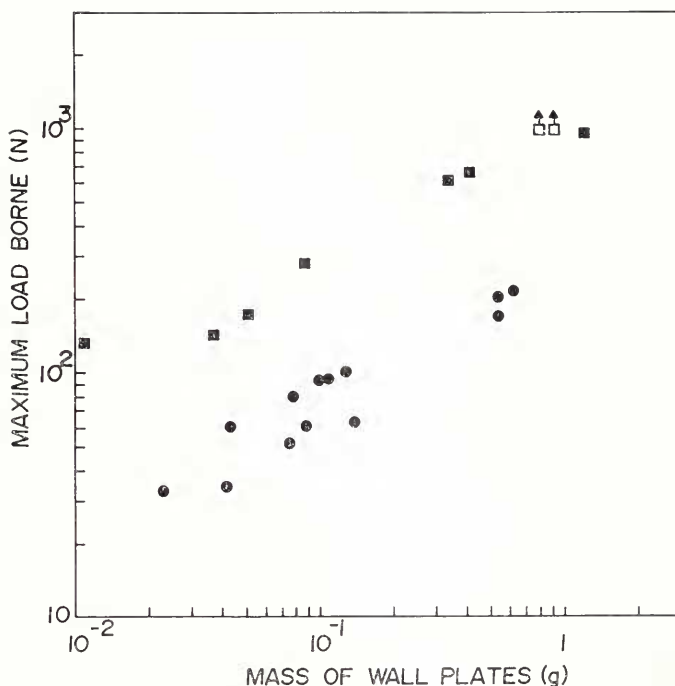
FIGURE 2. Shell strength expressed as the maximum load borne as a function of the mass of the shells for *B. balanus* (squares) and *S. balanoides* (circles). The two open squares indicate minimum values for two specimens of *B. balanus* which did not collapse under the maximum load which we were able to measure (1000 N).

measured. The height was taken from the base at a point mid-way along the rostro-carinal axis.

The head of the testing apparatus descended at 1 mm/minute, and the shells were loaded for a total of about a minute before they collapsed. The loading was usually not continuous; the head was moved up periodically to see what damage had been done.

The following measurements were made: maximum load borne; and the work done on the specimen up to the point of maximum load. The work was taken as the area under the load/deformation curve. This is the same as the energy absorbed by the specimen, the shaded area in Figure 1a.

After the test, the shells were cleaned for 24 hours in warm dilute KOH. The opercular plates were discarded, since they can have provided little strength in the mode of testing used. The shell plates were washed repeatedly and dried in an oven at 100° C before being weighed. The thin calcareous basis of *Balanus balanus* could not be weighed.

Figure 1a shows a typical load-deformation trace. This trace is idealized because usually the head applying the load was raised occasionally. When the specimen was reloaded, the load-deformation curve, instead of being jagged, usually rose smoothly up to the load that had been attained just before the head was raised.
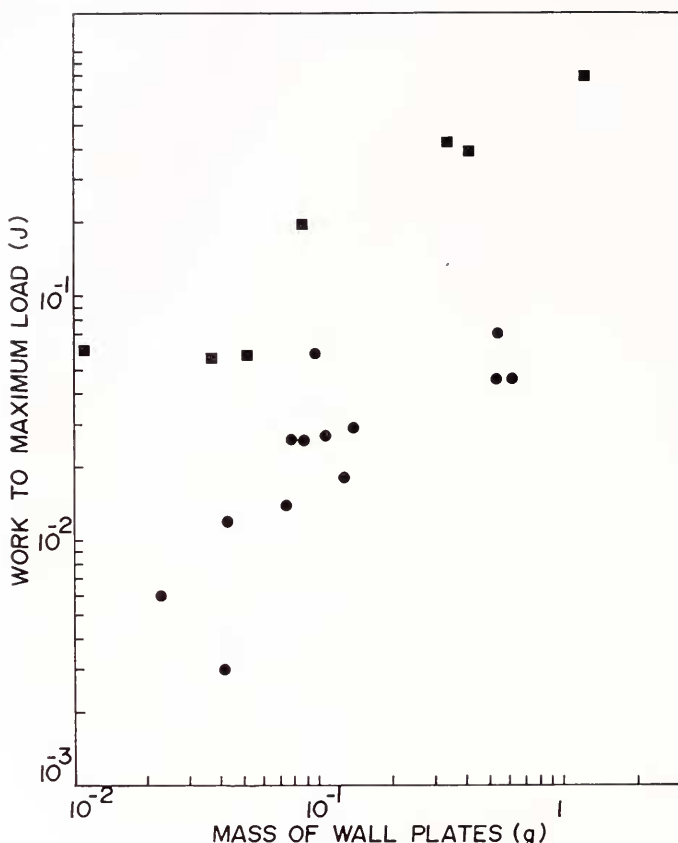
FIGURE 3. Shell strength presented as in Fig. 2 and expressed as the work done on the specimen up to the point of maximum loading (equal to the energy absorbed by the specimen). The two open squares indicate minimum values for two specimens of *B. balanus* which did not collapse under the maximum load which we were able to measure (1000 N).

This is reasonable evidence that the unloading-reloading cycle had not greatly altered the behavior of the shell. For purposes of calculating the energy absorbed, the area under the second curve up to the previously attained load was ignored (shaded in Fig. 1b).

Clearly, the larger the shell, the greater the load it should bear. Size was characterized in two ways: by the product of length and breadth and height of the shell, which we call pseudovolume; and by the mass of the dry, cleaned wall plates of the shell.

Scanning electron microscopy

Whole wall plates, fracture surfaces and etched polished surfaces were examined with the SEM. Polishing was accomplished with increasingly fine grades of carborundum paper and finished with alumina polishing paste on a felt pad. The polished
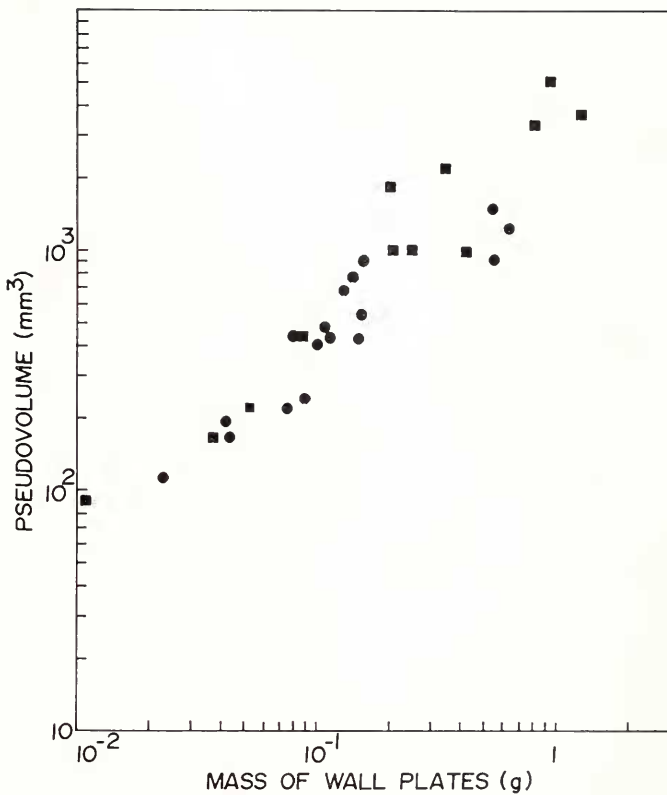
FIGURE 4. Shell pseudovolume (length × breadth × height) as a function of the mass of the wall plates for *B. balanus* (square) and *S. balanoides* (circle).

specimens were etched for a few seconds with very dilute hydrochloric acid. The specimens were then coated with gold.

Microhardness

Microhardness measurements were made with a Tukon microhardness tester which makes square-based pyramidal indentations with a diamond. The diagonals of the indentations were about 15 to 25 μm across, so differences between quite closely adjacent parts could be tested. The specimens were tested wet because dry mollusc shells, of similar composition, have been found to give higher values than wet ones (Currey, 1976).

RESULTS

Mechanical testing

The results of our mechanical tests show that for a given size, shells of *B. balanus* are consistently several times as strong as those of *S. balanoides*. This is

TABLE I

Results of compression tests on whole shells.

	Size (mm)			Shell Mass (g)	Max Load (N)	Work (J)
	Length	Breadth	Height			
Balanus balanus	19	17	7	0.341	618	0.433
	20	19	10	1.223	965	0.831
	18	17	17	0.916	>1000	—
	14	12	6	0.418	672	0.392
	18	21	9	0.796	>1000	—
	7	8	4	0.052	174	0.057
	7	6	4	0.037	144	0.056
	11	10	4	0.087	282	0.197
	5	6	3	0.011	132	0.060
Semibalanus balanoides	11	12	6	0.140	64	0.029
	11	12	5	0.129	103	0.018
	11	10	2	0.088	62	0.026
	10	11	4	0.099	93	0.058
	11	11	4	0.108	95	0.027
	10	11	4	0.078	80	0.026
	10	11	2	0.075	52	0.014
	17	16	10	—	390	0.136
	7	8	2	0.023	33	0.006
	7	8	3	0.043	61	0.012
	8	8	3	0.042	35	0.003
	16	13	6	0.626	219	0.046
	14	13	8	0.539	204	0.046
	13	12	6	0.540	180	0.071

true whether strength is expressed as the maximum load borne by each shell or as the work done on the shell by the applied load up to the point of maximum loading. Figure 2 shows the relationship between the maximum loads borne and the masses of the shells. Figure 3 shows the relationship between the work done by the applied

TABLE II

Relationship between dependent and independent variables. L is the maximum load in Newtons; V is the pseudovolume in mm³; W is the work in Joules done up to the point of maximum loading; and M is the dry mass of the shell in grams.

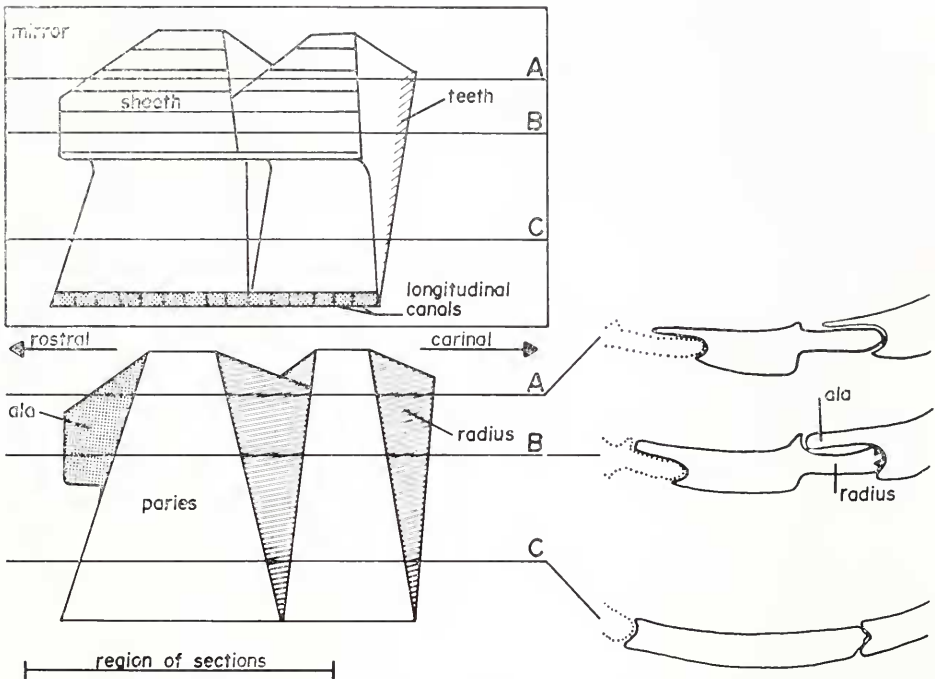| Species	Relationship	F	d.f.	P	Coefficient of determination
B. balanus	$\log L = 0.95 + 0.571 \log V$	83.3	1, 6	≪0.001	0.94
S. balanoides	$\log L = 0.15 + 0.674 \log V$	48.2	1, 13	<0.001	0.81
B. balanus	$\log L = 2.96 + 0.488 \log M$	91.2	1, 6	≪0.001	0.95
S. balanoides	$\log L = 2.44 + 0.561 \log M$	89.8	1, 12	≪0.001	0.89
B. balanus	$\log W = -2.89 + 0.781 \log V$	66.6	1, 6	<0.001	0.93
S. balanoides	$\log W = -3.90 + 0.851 \log V$	25.3	1, 13	<0.001	0.59
B. balanus	$\log W = -0.15 + 0.651 \log M$	38.9	1, 6	<0.01	0.89
S. balanoides	$\log W = -1.01 + 0.697 \log M$	18.5	1, 12	<0.001	0.63

FIGURE 5. Stylized diagrams of two lateral wall plates from *B. balanus*. The outer aspect is shown below and the inner is shown above as reflected in a mirror. To the side are shown the outlines of frontal sections at various levels in the shell.

loads up to the points of maximum loading and the masses of the shells. Pseudo-volume and mass are highly correlated (Fig. 4). Taking the values of *B. balanus* and *S. balanoides* together, the correlation coefficient is 0.96, and the shell mass is proportional to pseudovolume to the 1.13 power, showing that there is near isometry between shell mass and pseudovolume over the range examined. Because pseudo-volume is highly correlated with shell mass, we have not provided figures on its relationship to shell strength. The dimensions of the shells, their masses, and the two measurements of strength for each are presented in Table I. Table II shows the linear regression relationships between the dependent and independent variables which appear in Table I together with the relevant statistics. The last column in Table II shows the coefficient of determination or goodness of fit for each regression. This statistic is never less than 59% for *S. balanoides* nor less than 89% for *B. balanus*. For both species, therefore, a large proportion of the variation in strength can be explained in terms of variation in shell mass or pseudovolume.

The forms of the load-deformation curves were generally similar between the species, resembling Figure 1. There was an initial steeply rising phase with a few small reductions in load caused by the breaking of the irregular peaks around the operculum. The crosshead of the Instron moves with a constant speed, so a
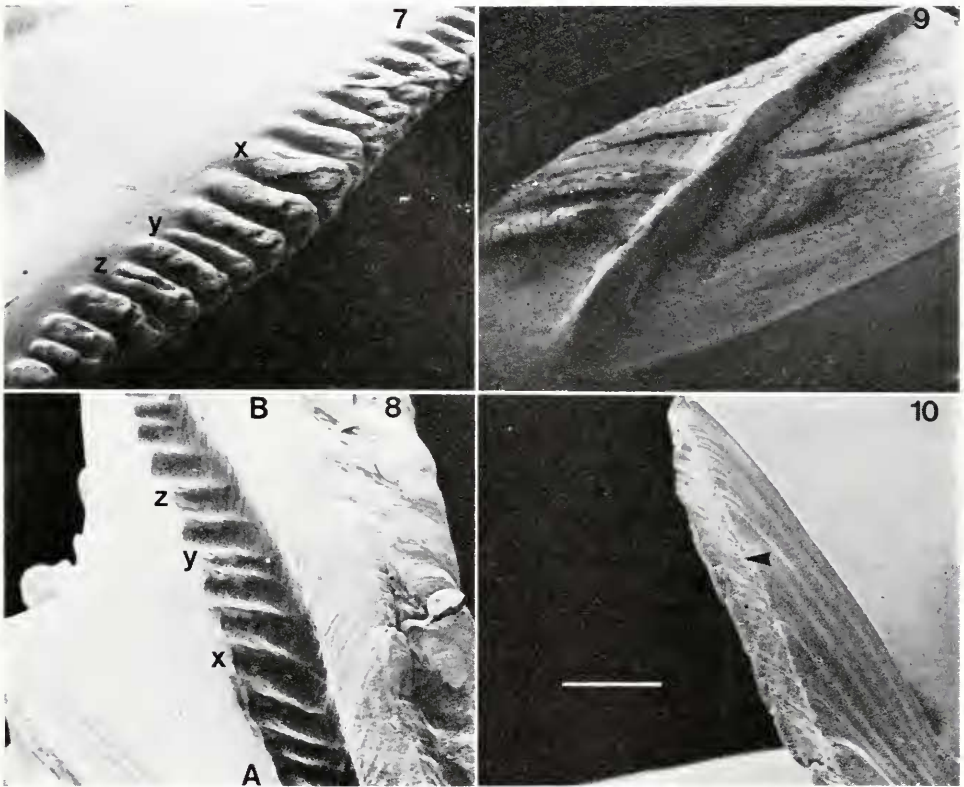
FIGURE 6. A scanning electron micrograph of the junction between the distal margin of a radius of *B. balanus* and the neighboring plate. A layer of cuticle can be seen between the two opposed surfaces. The section is parallel to the basis. The scale bar represents 20 μm.

crack in the specimen produces a sudden reduction in the load rather than a sudden increase in deformation. After the steep phase there was either a gently rising or a gently falling phase, again with frequent small reductions in load. The load sometimes declined slowly, nearly to zero, but at other times there occured a sudden large decrease in load; this was more often seen in *B. balanus* than in *S. balanoides*.

After the crushing down of the high points of the shell, one of the plates would eventually crack. Although the junctions evident between the plates would seem the natural place for the plates to fail, overt failure rarely began there; the first sign of failure was seldom the obvious moving apart of a pair of plates. Nevertheless, a slight movement of a junction, imperceptible to us, could throw an intolerable load on the neighboring plate by causing the load on the plate to be transmitted to the substrate at one place only. Usually failure of the shell would start with one of the plates cracking from top to bottom. It is not possible to tell whether the crack ran up or down. Once this happened the shell would start to disintegrate, with plates moving apart at the junctions and cracking, for the most part longitudinally. There was no really obvious difference in the mode of failure of the two species except that, once *S. balanoides* started to break, the plates seemed to move apart at the base more readily than did those of *B. balanus*.

Twice in testing large *B. balanus* (pseudovolumes of 3402 mm^3 and 5202 mm^3) the load exceeded the 1000 × limit of our instrument without destroying the shell being tested (Table I and Fig. 2). In each case, the top of the shell was greatly crushed, but damage did not extend down to the point where the hypodermis joins the shell wall. The crushed part of the shell had broken as a series of flakes approximately parallel to the inner surface of the sheath. The animals appeared unharmed, pumping and feeding normally when replaced in sea water.

FIGURES 7–14. Low power scanning electron micrographs of the wall plates of *B. balanus* and *S. balanoides* (at approximately the same magnification) showing the major features of the plates important in the formation of junctions with neighboring plates. Scale bars on Figures 10 and 14 represent 400 µm.

FIGURE 7. The ridged edge of the radius on a carinolateral plate of *B. balanus;* x, y, and z mark ridges which correspond to similarly marked pits on Figure 8.

FIGURE 8. Pitted groove along the edge of the paries of the carina of *B. balanus.* This receives the edge of the radius in Figure 7; x, y, and z indicate pits which correspond to similarly marked ridges in Figure 7. A and B mark the apical and basal ends, respectively.

FIGURE 9. Groove in the sheath region of the carinolateral plate of *B. balanus* which receives the ala of the carina. Note that it is smooth.

FIGURE 10. Rostral edge (indicated by arrow) of the ala on the carina of *B. balanus.* Note that it is fairly smooth.

Morphology of B. balanus

Figure 5 presents a highly stylized representation of the inner and outer aspects of a pair of lateral wall plates of *B. balanus.* The perspective has been deliberately distorted to make the plates appear flat in order to emphasize certain morphological points which are not easily seen in drawings of more realistic perspective.

Each radius abuts the adjacent plate near its apex and is in contact with it for virtually the whole height of the shell (Fig. 5). The carinal margin of each radius is received snugly in a groove along the edge of the paries of the next plate, just
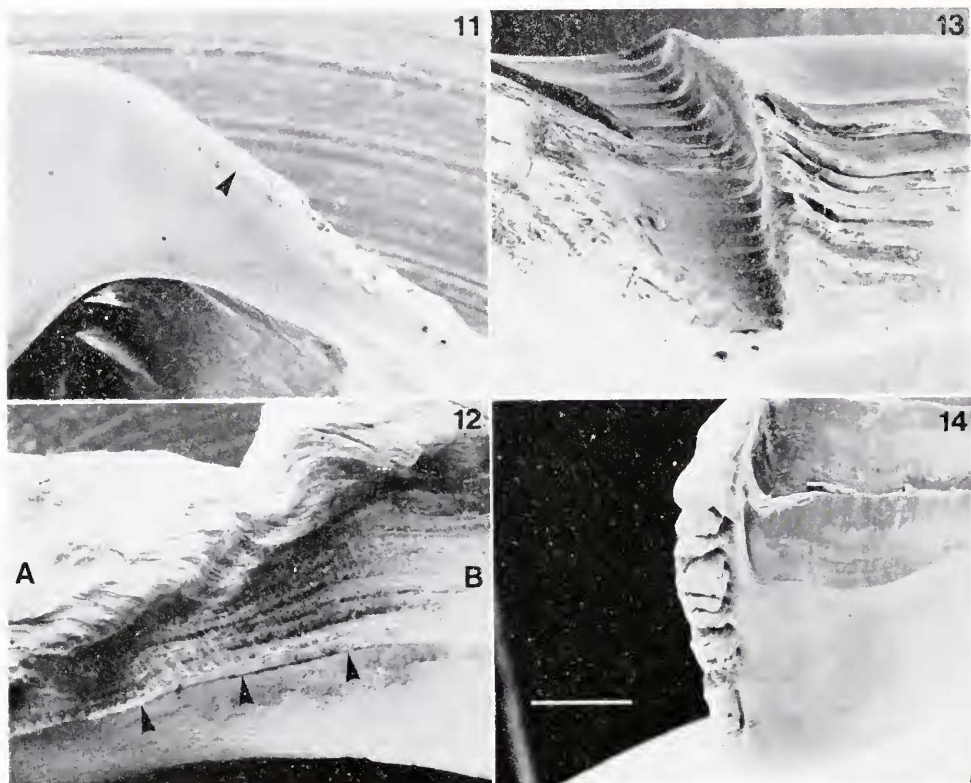
FIGURE 11. Inner surface of the radius on the carinolateral plate of *S. balanoides*. Compare its even edge (arrow) with the corresponding structure in *B. balanus* (Fig. 7).

FIGURE 12. Margin of the paries on the carinal plate of *S. balanoides* where the edge of the radius of the carinolateral butts against it. Contact begins along the line indicated by the arrows and extends as a snug abutment for a short distance only in the direction of the tails of the arrows. The region figured is a little below section A in Figure 23. A and B indicate the apical and basal ends of the structure, respectively.

FIGURE 13. Groove in the sheath region of the carinolateral plate of *S. balanoides*. The shallow pits receive the teeth on the rostral margin of the ala of the carina.

FIGURE 14. The roughly toothed rostral margin of the ala on the carina of *S. balanoides*.

outside the base of the ala. (Snug is defined here as the condition in which the two plates fit tightly up against each other, with the interposition of only a very thin layer of organic material, a few microns thick; Fig. 6.) The inner surface along the radius is ridged (Figs. 7, 15), the ridges projecting somewhat beyond the end as teeth. These ridges are probably basically the same as those figured by Darwin (1854) for *B. tintinnabulum* [*Megabalanus tintinnabulum* (Newman and Ross, 1976)] and strikingly similar (especially in Darwin's figures) to the teeth at the base of the paries which give rise to the so-called interlaminate figures (Newman, Zullo and Wainright, 1967). These ridges fit into shallow pits in the bottom of the groove on the paries, which groove receives the edge of the radius (Figs. 8, 16). The tips of the ridges often have a chalky white appearance. The radius

doubtless continues to grow towards the carina along this margin, this growth having the effect of pressing the ridges into their pits and widening the opercular opening of the shell.

The alar margins slope from the apices of their plates rostrally and basally until they abut a ridge running perpendicular to the basal margin of the sheath on the next more rostral plate. This ridge often forms a shallow groove (Figs. 9, 17) which receives snugly the rostral margin of the ala much as the carinal margin of the radius is received. The ala, unlike the radius, is not strongly ridged though the rostral edge may be slightly knobbly or lumpy (Figs. 10, 18). The material forming the rostral edge of the ala is chalky white, very reflective and opaque both when seen as a complete plate, and in polished sections. The rest of the plate material is substantially more translucent.

Between the overlapping radius and ala, in the mid-region of the overlap when viewed in section (as in Fig. 5), is a narrow space. Smaller spaces occur near the ends of these projections where they form snug abutments with neighboring plates. Except in their upper regions these spaces contain tissue in life (see Costlow, 1956).

Below the level of the sheath, the radius still forms a ridged projection on the carinal margin of each wall plate. This is received in a matching shallow pitted groove on the abutting plate. Along the base of the plate, the bases of the longitudinal septa form teeth which interlock with holes on the calcareous basis, formed at the ends of radiating canals, as described by Darwin (1854), and Newman et al. (1967). There is a thin layer of tissue between the plates and the basis.
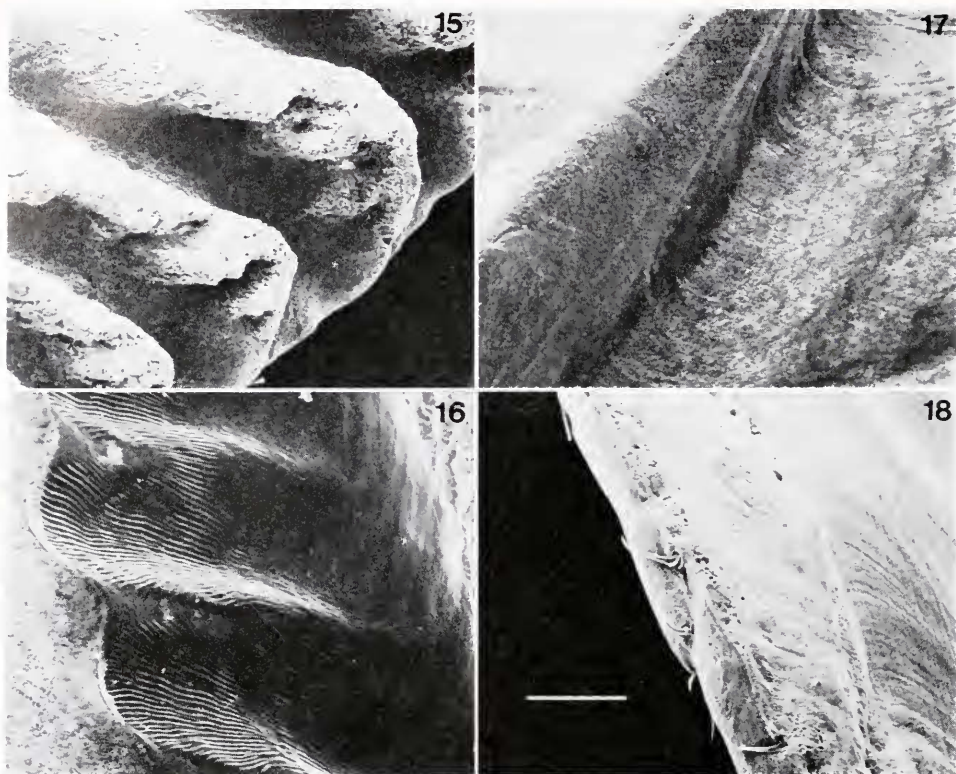
Morphology of S. balanoides

Figure 23 presents a stylized view of two plates from the shell of *S. balanoides,* drawn in the same manner as Figure 5. More realistic drawings of the wall plates of *S. balanoides* are to be found in Stubbings (1975). Other diagrams are available in Gutmann (1960).

Compared with *B. balanus,* the radius is much less prominent, forming little more than a narrow strip along the carinal edge of the paries (Figs. 11, 19). The inner surface, near the edge of the radius, may meet the outer surface of the underlying ala in a flat junction, but the margin of the radius is typically not received in a groove except perhaps very near the base of the shell (Figs. 12, 20). This is in marked contrast to *B. balanus.*

It appears from our sections that the carinal margin of the radius is often not in close contact with the ala though this may possibly be an artifact. The inner surface of the radius consists of chalky white material similar in appearance to that described above on the edge of the ala in *B. balanus.*

The ala is very much stouter than the radius. It is roughly square-ended both in profile (inner or outer surface) and in section. The rostral margin abuts the next shell snugly over much of the height of the sheath region. This is in contrast to *B. balanus* where only the lower part of the alar margins abuts the neighboring plate. The portion of the rostral margin nearest the overlying plate is again chalky white and lumpy, and may have some teeth (Figs. 13, 14, 21, and 22). In the central part of the overlap between the ala and the overlying portion of the neighbor-

Figures 15–22. Higher magnifications of the areas shown in Figures 7–14. The scale bars on Figures 18 and 22 represent 100 μm.
Figure 15. Edge of the carinolateral radius of *B. balanus.*
Figure 16. The pits in the groove on the carina of *B. balanus* which receive the radius of the carinolateral. Note that the pits themselves have ridges.
Figure 17. Groove in the sheath of the carinolateral plate of *B. balanus* which receives the ala of the carina.
Figure 18. Rostral edge of the ala on the carina of *B. balanus.*

ing plate is a substantial gap except in the areas of snug fit mentioned above. Again, as in *B. balanus*, except in its upper part, this gap is filled with tissue in life.

Below the sheath, the wall plates butt up tightly against each other, usually showing little sign of geometric locking devices. There is no calcareous basis, and the plates fit down against the substratum with only the thin membranous basis intervening.

Shell microstructure

Most of the material of the etched specimens of both species appeared very similar to that which, in molluscs, is termed 'homogeneous' (Taylor, Kennedy, and Hall, 1969). This is characterised by roughly isodiametric grains which, in these barnacles, are of the order of 1 μm in diameter. It is quite possible, of course, that these "grains" may be polycrystalline, but our scanning electron microscope could

not resolve better than about 0.1 μm. In places, in the radius and ala of *B. balanus* and in the ala of *S. balanoides*, there are elongated crystals of the order of 1 μm in diameter and more than 10 μm long. These form fan-like arrays reminiscent of spheritic growth forms in scleractinian corals (Bryan and Hill, 1941; Jell, 1974). Where they occurred near the surface of the plate they were approximately perpendicular to it (Fig. 6). These arrays of long crystals frequently show transverse banding, probably indicative of variations in growth rate.

The chalky marginal areas of the wall plates, which are shown below to be soft, are very fine-grained (grain size approximately 0.5 μm) while the harder translucent areas show the normal larger grain size characteristic of the rest of the plate.

Microhardness

Tests were carried out both in the vicinity of junctions in the sheath region and on the parietes. Readings taken *very* close to a junction or an edge tended to
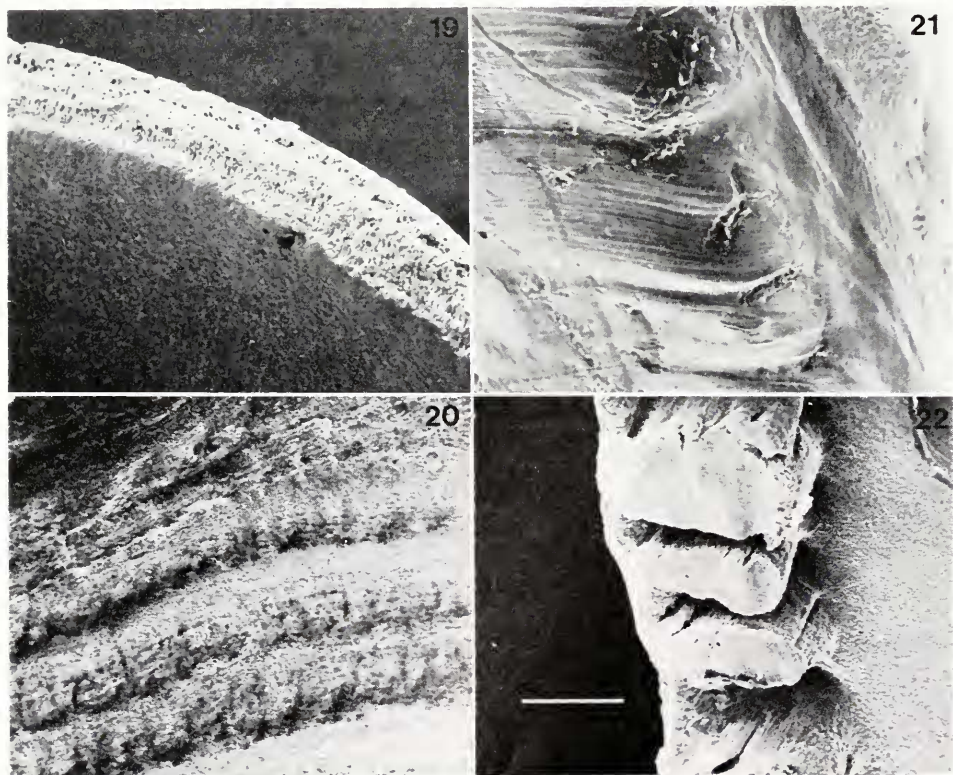

FIGURE 19. Edge of the radius on the carinolateral plate of *S. balanoides*.

FIGURE 20. Region on the carina of *S. balanoides* where the radius of the carinolateral plate butts against it.

FIGURE 21. Shallow pits in the groove in the sheath region of the carinolateral plate of *S. balanoides* which receive the teeth on the rostral edge of the ala of the carina.

FIGURE 22. Teeth on the rostral edge of the ala on the carina of *S. balanoides*.
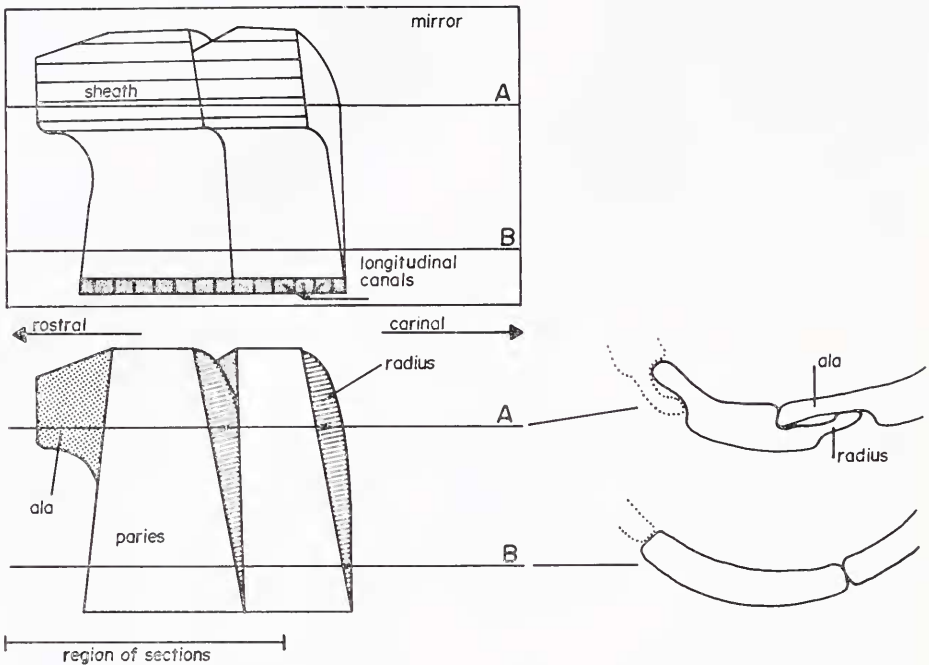
S. balanoides

FIGURE 23. Stylized diagram of two lateral wall plates from *S. balanoides,* presented as in Figure 5.

be lower than elsewhere, probably because the proximity of a free surface to one side of the indentation allows the material to deform more easily in that direction. Therefore, readings taken within about 50 μm of a junction are excluded from these results.

Tests were made on surfaces in three different orientations: parallel to the plane of the basis (frontal); tangential to the shell as a whole (tangential); and radial to the shell as a whole (radial). These last tests were an attempt to measure the hardness of the junctions in the direction in which they would be loaded by the adjoining plate.

Microhardness tests were done on ground and polished frontal surfaces of the parietes in the sheath region for all six plates from one specimen of each species. The results are given in Table III, denoted by "paries far from junction". The means are not significantly different. Even if the difference between the means were real, it would suggest quite trivial differences in the mechanical properties of the shell materials.

In some places, usually close to junctions, the shell was chalky white instead of translucent or grey, as it was in other places. We expected that there might be differences in michhardness accompanying these optical differences. In tangential and frontal surfaces it was difficult to ensure, first, that one was not loading a

<div align="center">TABLE III</div>

The hardness of shell material in various regions and various orientations.

Species	Part	Orientation	Mean hardness	n	s.e.
B. balanus	Paries, far from junction	Frontal	245.9	32	5.03
	Paries, near junction	Frontal	276.6	11	6.25
	Radius, near junction	Frontal	253.6	16	11.00
	Radius, toothed edge	Radial	223.5	20	6.6
	Groove on paries receiving radius	Radial	217.3	16	6.5
	Anterior edge, ala (chalky)	Radial	113.2	9	11.3
	Anterior edge, ala (translucent)	Radial	215.3	7	8.6
	Posterior edge, radius	Tangential	231.7	10	10.0
	Paries (where radius butts against it)	Tangential	242.0	7	14.3
S. balanoides	Paries, far from junction	Frontal	235.5	30	3.0
	Paries, near junction with ala	Frontal	235.1	7	11.5
	Ala, near junction with paries	Frontal	242.3	6	13.5
	Distal edge of radius	Radial	173.8	8	10.5
	Anterior edge, ala (chalky)	Radial	199.2	10	6.1
	Anterior edge, ala (translucent)	Radial	323.5	6	6.7
	Anterior edge, ala	Tangential	202.6	10	9.8
	Paries (where ala abuts)	Tangential	245.7	10	14.6

chalky region that was in fact overlain by, or overlying, a thin layer of translucent material and secondly, that one was not loading very close to an edge of the chalky material.

Therefore, we have not distinguished between chalky and translucent regions in tests on frontal and tangential surfaces. On radial surfaces, however, the differences in microstructure were clear, and the two are distinguished in the results presented in Table III.

In general, the microhardness values varied from region to region in a not very predictable way (Table III). The one consistent difference was that on radial surfaces the chalky region was softer than the translucent region next to it. An example from each species is shown in Figure 24, with the locations and values of the hardness tests indicated. The rather high values for *S. balanoides* are unusual, not being seen elsewhere in either species.

DISCUSSION

The shells of *B. balanus* are about three to thirteen times as strong as those of *S. balanoides,* depending on the variables considered. This difference in strength is very unlikely to be due to the mechanical properties of the materials in the shells of the two species and is probably due to differences in the large-scale architecture of the wall plates and bases of the shells.

The differences in the bases provide the most obvious, and possibly the most significant mechanical difference between the shells of the two species. *S. balanoides* shells are kept on the substratum merely by the strength with which they are attached to the membranous basis, which is in turn firmly glued to the substratum (Stubbings, 1975). In *B. balanus,* although there is tissue between the wall plates
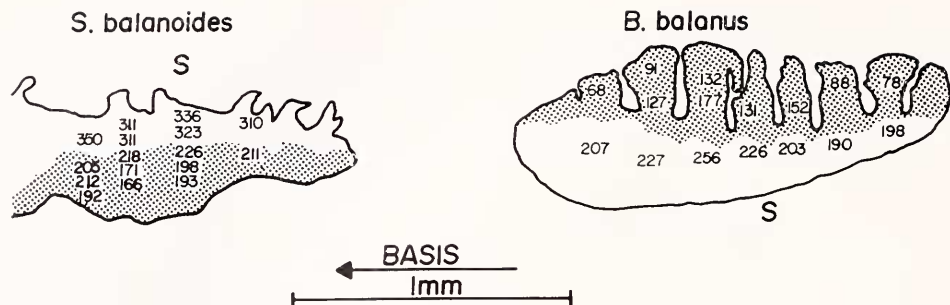
FIGURE 24. Radial sections (perpendicular both to the basis and to the shell wall) at the distal margin of an ala from each of *B. balanus* and *S. balanoides*. The stippling indicates the opaque white areas in the specimens, unstippled areas were translucent. The numbers are microhardness values and each is centered on the location of the test it represents. The letter S indicates the sheath side of the section. In each case, the basis of the shell is to the left, and the apex to the right.

and the calcified basis, there is a fairly complex system of interlocking buttresses (Newman *et al.*, 1967) that anchor the shell to the basis which is firmly glued to the substrate.

There is a well-known tendency of *S. balanoides* to grow in serried masses, with a resulting likelihood of peeling off the substrate in great sheets (Connell, 1961; Barnes and Powell, 1950). It is possible that the mechanical importance of the basis of *S. balanoides* should be considered in this context. The lack of a calcified basis will be less important, from the point of view of resisting direct loading, in an animal which is supported on all sides. Calcified bases will help stop the feet of the plates from slipping outward as the result of loads from on top. In *S. balanoides* (or in any other species) if the feet of the plates are jammed up against adjacent shells, the lateral support function may be taken over by those shells. This does not mean, of course, that a calcareous basis would not be useful. It could be that, for isolated individuals, and even in massed individuals, a more-or-less common calcified basis would help prevent the whole mass from being dislodged.

The wall plates differ between the two species in a characteristic which seems best described as workmanship. Workmanship is defined here as regularity and precision in the details of construction, particularly in the design of the joints between plates.

There is a difference in workmanship between the two species which is particularly clearly visible in uncrowded specimens. This is that the external form of *B. balanus* is much more regular than that of *S. balanoides*. *B. balanus* has a neat volcanic shape with sharp radiating ridges. Growth arrest lines are not readily visible. *S. balanoides* is, in general, lumpy, with clear growth arrest lines and overhangs. Whether these differences are mechanically important cannot be proven, but irregularities such as overhangs and bumps contribute little to the strength of a structure, and could even create local stress concentrations, weakening it. Although, when loaded slowly, the shells of these barnacles seem not to come apart first at the junctions between the plates, it is likely that the integrity of the junctions is of paramount importance to the animals. Barnes *et al.* (1970) claim that they do

come apart first at the junctions when loaded laterally. Effectively any kind of loading will, because of the irregularities in the shell, tend to make some of the wall plates shear past each other at their junctions. If the junctions are rigid, the shell will continue to bear the load as a whole. If, however, the junctions have some play, they will allow the plates to rock slightly relative to each other and relative to the substrate. This rocking will produce very high local stresses, often at points well removed from the junctions.

The difference between the two species in the strengths of the junctions between wall plates was qualitatively obvious. During the preparation of specimens of the two species for sectioning and microscopical examination, there was a much greater tendency for *S. balanoides* simply to fall apart at the junctions than for *B. balanus* to do so, even when the calcareous basis of *B. balanus,* which gave considerable coherence to the shell, had been removed.

The distal margin of the radius of *B. balanus,* where it abuts on the neighboring plate, is received in a groove (Fig. 5). Such a junction (which we shall call a *dado,* as do Barnes *et al.,* 1970), restricts possible disarticulating movements of the two opposed surfaces in the plane of a frontal section to one direction only, roughly parallel to the ala itself. Disarticulating motion in any other direction must break one of the two plates. So long as the opposing surfaces of the junction are held together, this will be a very strong type of junction.

A dado joint at the carinal margin of the radius of a plate of *B. balanus,* and the strong teeth on ridges along that margin, make the junction between that and the neighboring plate a strong one. The teeth increase the surface area of contact for adhesion and also prevent slippage parallel to the junction. Our scanning electron microscope results show a cuticular layer between the surfaces at this junction which may act as an adhesive, and probably seals the junction against invading organisms (Fig. 6).

The carinal margin of the radius in *S. balanoides,* on the contrary, contacts the paries of the neighboring plate along its basal portion only, where it makes a flat or very shallowly-grooved junction. Therefore, the junction must be much weaker than the equivalent one in *B. balanus.* The upper margin may in places be closely opposed to the outer surface of the underlying ala and this region need not be thought completely devoid of strength. There is, however, no mechanical interlocking of the radius and ala. Therefore, the construction of the radial-parietal junction is much more precise in *B. balanus* and resists relative movement of neighboring plates by its geometrical arrangement. This is in strong contrast to *S. balanoides.*

The general form of the junction between the distal edge of the ala and the neighboring plate is similar in the two species. The length over which the junction is snug when compared with the height of the sheath region is somewhat greater in *S. balanoides* than in *B. balanus.* However, when the ala of *B. balanus* forms a snug junction it is often a snug dado, whereas the homologous junction in *S. balanoides* is never of this geometrically locking type.

In a sense the morphological pattern in the sheath region of the junction between the plates of *B. balanus* is the reverse of that in *S. balanoides* [compare frontal (horizontal) sections in Fig. 5 level B and Fig. 23 level A]. In *B. balanus* the strong, interlocking part of the junction is formed by the radius. In *S. balanoides*

it is formed by the ala and, hence, cannot be longer than the sheath and is usually rather less. In comparing the strong parts of these two junctions, it is apparent that the margin of the radius of *B. balanus* always forms a good dado, geometrically interlocking joint, while the square-ended margin of the ala of *S. balanoides* usually does not. In *S. balanoides* the radius, and in *B. balanus* the ala, may form snug junctions along their distal margins but not such strong ones.

We can only speculate why the radius or the ala should be preferred for the strong part of the junction. There is no obvious important mechanical reason to prefer one design over the other in the sheath region, although, of course, the strong toothed and ridged radial joint of *B. balanus* extends below the sheath region. All else being equal, the more exposed surface of the junction seems more likely to be attacked by organisms. Thus a snug junction at the margin of the radius may be very important, not only for mechanical reasons, but also in preventing the ingress of potentially destructive organisms.

The outer surface of *S. balanoides* is often badly corroded by weather and abrasion through wave action, common in the high energy intertidal environment. To put a strong junction on the outward facing surface (the sheath, too, is actually external to the mantle cavity and exposed to the environment) may be to put it where it is likely to be destroyed no matter how well designed and constructed. Natural selection may have favored placing the stronger junction at the inner surface of the sheath region in *S. balanoides* to shield it from damage.

Junctions may be held together by adhesives as well as by their geometry. There is evidence of a very thin layer of organic material, presumably adhesive, in some junctions (see Fig. 6). In general, junctions held together by adhesives are strong only if the two glued surfaces are closely apposed (Gordon, 1976). This may be an important aspect of the mechanical design of these junctions which we refer to as "snug." Bocquet-Védrine (1965) claims that extensions of the cuticle of the animal may serve as an adhesive in some junctions.

B. balanus, therefore, is consistently more regular and precise of construction than is *S. balanoides; B. balanus* has superior workmanship. This greater regularity and precision must contribute to the greater strength seen in the shells of *B. balanus.*

The resistance of *B. balanus* shells to crushing was strikingly shown in the two specimens which resisted 1000 N by the flaking of the top of the sheath rather than cracking. This may represent a mode of nondisastrous, controlled collapse which allows large animals to absorb the energy of impact without failure. Additionally, such flaking may increase the surface area bearing the load, thereby decreasing *local* stresses and the likelihood that a disastrous crack will start.

Although the shells of *B. balanus* and *S. balanoides* differ in their construction and workmanship in a way that might account for the observed differences in strength, it is also possible that differences in the mechanical properties of the shell material itself might make a substantial contribution to the differences in the properties of the whole shells. Differences in the mechanical properties of molluscan shell materials are due to differences in the microstructure of those materials (Currey, 1976, 1977; Currey and Kohn, 1976). The constitution of barnacle shells is similar to that of molluscs (Bourget, 1977; Barnes, Klepal and Mitchell, 1976; Wilbur and Simkiss, 1968). Thus, if the observed large difference in strength between

the two species is due to differences in material properties, a significant difference in microstructure should be seen between the two.

It is remarkable, therefore, that the macroscopically and mechanically dissimilar shells of these two species are so very similar at the microstructural level. It is very unlikely that two materials so similar in microstructure should differ sufficiently in mechanical properties to explain the overall differences in strength which were measured.

Despite the ultrastructural similarity of the materials in the plates in the two species, we wanted to measure and compare the mechanical properties of the plate materials. Because the plates themselves are of such irregular shape, we judged conventional compression, tension or bending tests unlikely to yield useful results (see Wainwright, Biggs, Currey and Gosline, 1976). Hardness tests, however, were possible on small, polished specimens. Hardness is not a well understood feature of materials. It is not easily related to other mechanical properties, but it seems to depend on the modulus of elasticity and the yield strength in compression (Mott, 1956). Thus, if the observed difference in overall strength between species was largely attributable to differences in mechanical properties of the materials of the shell of the two species, this difference should be reflected in microhardness tests. The values given by the tests can be considered as arbitrary, as we are interested only in comparisons between the two species.

Although mechanically important variations in hardness within the shells may be demonstrable, there is no general difference between the species which could explain the observed differences in overall strength. This is again remarkable in light of the difference in overall properties of the two shells, but, like the ultrastructural results, argues strongly that the observed differences in shell strength are not due to differences in the properties of the shell material.

In lateral impact loading Barnes *et al.* (1970) found that *B. balanus* was stronger that *S. balanoides*, though only by about 50% or so at the greatest, and they indicate (their Fig. 2) that at small sizes *S. balanoides* is slightly stronger than *B. balanus*. They performed some impact tests on cantilever test pieces cut from shell plates, and could find no large difference in "momentum per unit area" resulting in fracture. They conclude (p. 82) that "since the strength of the wall plates *per se* for animals of the same size has been shown to be similar any distinction between the species must arise as a result of differences in strength at the junctions." This seems a rather sweeping conclusion, since a number of other things could affect the strength of the whole shell: the shape of the plates, the shape and construction of the whole shell, and the mode of attachment of the shell to the substrate. We agree with Barnes *et al.* (1970) that junction morphology is an important factor in determining junction strength. Their means of characterizing the morphologies of the junctions by describing sections of the shells taken at "mid height" is likely to lead to erroneous conclusions, however. It is clear from their published pictures that they are comparing junctions from the sheath region of *S. balanoides* with those from below the sheath in *B. balanus*. Inspection of the disarticulated wall plates will show that an understanding of the shape of the junction between two plates is possible only with sections from at least two levels (Figs. 5 and 23): in the sheath region and below it. Also, unevenness of the substratum often results in asymmetry in the growth of a barnacle. Unless care is

taken under such conditions, a section taken through the shell near mid height is likely to pass through two distinct regions of the shell which differ markedly in their morphology. Several such sections are presented by those authors; in particular, the sections of *Chthamalus stellatus*, *Semibalanus balanoides* and *Balanus crenatus* pass partially through the sheath and partially below.

Our results cannot be compared directly with those of Barnes *et al.* (1970). They determined the height from which a metal load of known mass must be dropped just to break the shells and calculated the approximate momentum of the bar at the moment of impact, whereas we loaded slowly. Furthermore, we loaded the specimens on top, whereas they loaded them from the side. While they indicate the range of sizes available for testing for each species in their Table 1, several of the regression lines in their Figure 2 extend beyond the ranges given. Thus, it seems clear that they did not determine that small (*ca.* 2.5 mm diameter) *B. balanus* and *S. balanoides* have the same strength as their Figure 2 indicates, since the smallest *B. balanus* available was 3.5 mm in diameter. The largest whole shell tested for each of these two species was 12 mm in diameter. As *B. balanus* commonly gets substantially larger than this, their sample does not appear to be representative of the species. They tested individual wall plates from *S. balanoides* 16–23 mm in diameter and from *B. balanus* 15–26 mm in diameter. It is unfortunate that some of these large specimens were not used to test the strength of whole shells. The number of specimens tested is not given, and so we cannot calculate the probabilities associated with the correlation coefficients they give, which are all very high. Barnes *et al.*, used high-speed ciné photography on a specimen of *S. balanoides*, which it is claimed shows that the junctions open before the plates crack. This is possibly the case, although the situation is by no means clear.

Given these various facts, it is not certain whether, for instance, *B. balanus* was determined by Barnes *et al.* (1970) to be weaker than *S. balanoides* at lower sizes as the crossing over of the regression lines would indicate, and whether the differences we observed in the higher size ranges were seen by them.

Since, when tested by our method of loading, *B. balanus* is so much stronger than *S. balanoides*, it is perhaps appropriate to speculate what selective forces have led to the differences between the species. It should be emphasized that we know the strength of the two species from our locality and from particular tidal levels, and although much of the information we have obtained from the literature refers to similar locations, it is possible that the strength of the animals, and their condition of life, may be different elsewhere.

Our hypothesis is that once settled, *S. balanoides* is likely to be killed in the first or second season by an event unrelated to shell strength. *B. balanus,* on the other hand, appears to live, once established, for several seasons and hence is more likely to encounter situations in which shell strength is critical to survival. *S. balanoides,* therefore, channels its energies early, as early as the middle of the first year, to reproduction at the expense of other factors such as the workmanship of the shell. *B. balanus,* on the other hand, begins to reproduce later, typically in the second year, and so invests more heavily in a secure shell to help ensure a prolonged survival.

The energentic cost of building a calcified skeleton is, unfortunately, unknown. If a high degree of order is needed in the deposited calcite, precise control processes

will be needed which are likely to be energetically costly. For this reason, precise architectural construction may be costly for barnacles, and may be a significant fraction of the whole cost of building the shell.

In Britain *S. balanoides* is almost entirely intertidal, and *B. balanus* is sublittoral. The work of Grant (1977), Connell (1961), and Barnes and Powell (1950) shows that *S. balanoides* undergoes great fluctuations in population density. These fluctuations are produced by, among other things, overcrowding, which causes great sheets of consolidated shells to break off the substrate during storms (Barnes and Powell, 1950), depredation by whelks (Connell, 1961), sea ice, though rarely in Britain (Barnes, 1957), and even, for high littoral forms, calm hot days during neap tides (Connell, 1961). The result of these various sources of catastrophic death is that, from autumn to autumn, one may find patches of rock sometimes covered by *S. balanoides* approaching sexual maturity, and sometimes bare of barnacles. *B. balanus* rarely shows the gross overcrowding shown by *S. balanoides,* and it is almost certain that its environment, in British waters, is more stable from year to year.

In Britain *S. balanoides* shows little growth after one or two years (Barnes and Powell, 1953). Furthermore, the population of large *S. balanoides* is limited by predation by the whelk *Nucella lapillus,* which preys heavily on them in preference to smaller individuals. *B. balanus,* on the other hand, grows considerably after the first two years (Crisp, 1954). Data presented by Crisp indicate there is no sharp rise in mortality at any time during the first four years of life. Moreover, *B. balanus* does have a behavior pattern (Darwin, 1854; Crisp and Southward, 1961) which probably serves as an anti-predator device. The operculum can be tipped up and pressed against the sheath of the rostrum and lateral plates and rubbed from side to side. Any intruder who pokes at the opercular membrane is likely to be pinched between the opercular plates and the inner surface of the sheath. If *S. balanoides* is attacked, its only recourse is to close its opercular plates tightly. Being subtidal, *B. balanus* must have a shell capable of resisting attack from predators, such as crabs, which are less prone to venture into the high energy intertidal region (Kitching, Muntz, and Ebling, 1966).

Data derived from Barnes, Barnes, and Finlayson (1963) seem to indicate that *B. balanus* and *S. balanoides* produce a similar relative mass of sperm per season; the drop in body mass in the two species caused by the shedding of sperm (*ca.* 50%) is about the same (the "body mass" does not include the mass of ovarian tissue). However, Barnes and Barnes (1968) have calculated that the mass of eggs per unit body mass is about twice as great in *S. balanoides* as in *B. balanus.* This difference, though large, is subject to considerable experimental error, so should not be taken as very secure.

Calculations from data given in Figure 5 of Barnes *et al.* (1963) indicate that *B. balanus* grows a shell about two and a half times more massive, per unit dry body mass, than that of *S. balanoides.* This fits very well with our general view regarding the strength and general strategy of the two species. However, as Barnes *et al.* (1963) state, and Dr. Barnes (personal communication) has emphasized, these animals were grown under optimal conditions on rafts, and may not be very good indicators of the natural state of affairs. Furthermore, we performed some preliminary experiments in which the dry mass of the shell (excluding the

calcareous basis of *B. balanus*) was compared with the dry body mass (excluding the ovaries). These measurements were taken in early July, 1977; the animals came from situations in the Clyde Estuary similar to those of animals tested mechanically. There was an indication that in the smaller animals, with dry body mass of less than 5 mg, *B. balanus* had shells slightly more massive than those of *S. balanoides,* but that this difference disappeared when body weight reached about 10 mg.

If the actual masses of the skeleton per unit body mass are approximately the same, would it not be possible for *S. balanoides* to build as strong a shell as *B. balanus* and yet incur no penalty? Although there are good reasons for thinking that a strong shell might often be of little use to *S. balanoides*, it would surely be useful on occasion, and if no increase in cost were associated with a stronger skeleton, it would be selected for. Even if the weight of the basis were included in the calculations of shell weight, the skeleton of *B. balanus* would be so much stronger that selection in the direction of a *B. balanus* type of skeleton on the part of *S. balanoides* would seem to be of advantage.

Two possible explanations can be proposed as to why no such selection has occured. First, the shell of *S. balanoides* may be designed to meet criteria other than strength in resisting the sort of load we applied, perhaps having to do with growth under extreme crowding. The lack of a calcareous basis in *S. balanoides* may be related to its habitually crowded living conditions. Secondly, the cost of precise, strong shell construction may simply be greater than is warranted given the ecology and life history of these animals. If precise construction is expensive, and if early reproduction in *S. balanoides* is essential, the observed shell design would make sense.

The superior mechanical performance of *B. balanus* shell is attributable to the design and precision of construction of the skeleton, and to the calcareous basis but not, insofar as these microstructural and microhardness studies give any indication, to differences in the shell material itself. Unfortunately, there is no quantitative information on the biological cost of building something precisely. Sometimes time is a cost. In many molluscs relatively weak, prismatic material is laid down first at the rapidly growing margin of the shell and is then slowly reinforced with the stronger nacre (Taylor *et al.,* 1969; Yonge, 1953). In vertebrates, rather disorganized woven bone is produced quickly in areas of rapid bone growth, to be replaced more slowly later by more highly organized lamellar bone (Wainwright *et al.,* 1976). In these examples rate of growth is apparently related to skeletal organization, but the relationship remains, of course, to be demonstrated in barnacles. In the natural habitat, the shells of the two species grow at similar rates, but *B. balanus* is slower than *S. balanoides* in the early summer of the first year (Barnes *et al.,* 1963). Because of the microstructural similarities of the materials in the shells of the two species, this difference in growth rate is probably not due to a difference in the cost of shell material. The early rapid growth by *S. balanoides* may, however, be necessary to obtain the minimum size for reproduction during the first year, and it may take place at the expense of the workmanship and strength of the shell. In the first autumn *S. balanoides* is engaged in reproduction and *B. balanus* catches it up in size, presumably because it can devote relatively more effort to growth.

Summary

1. The shells of specimens of *Semibalanus balanoides* and *Balanus balanus* were loaded in compression. For shells of similar mass or pseudovolume ($1 \times b \times h$), *B. balanus* was about four times as strong as *S. balanoides*.

2. The morphology of the shell plates and their junctions is described. The shell of *B. balanus* is mechanically superior to that of *S. balanoides* in its possession of a calcified basis, well developed radii and in its general workmanship.

3. Neither the microstructure nor the microhardness of the shell plates gives significant indications that differences in material properties could account for the differences in strength observed.

4. It is suggested that *S. balanoides* has a life history with a short life expectancy which makes it important to reproduce early in life and that, compared with *B. balanus*, neatness of shell construction and, hence, shell strength is sacrificed to speed in the process.

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